A review of the Mexican Stoneroller, *Campostoma ornatum* Girard (Pisces: Cyprinidae)

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ABSTRACT.—A morphological study of the Mexican stoneroller, *Campostoma ornatum*, from throughout its range revealed that the species is distinctive in the genus *Campostoma* in having very small scales, breeding tubercles in the females as well as the males, and intestinal loops that rarely coil around the bladder. *C. ornatum* is extremely variable both in meristics and morphometrics, although populations from the southern part of the range tend to be more consistent in having fewer scales and deeper bodies. Because of its extreme and rather irregular variability, from drainage to drainage, intraspecific taxa, including *C. ornatum pricei* are not recognized. *C. ornatum* displays several generalized characters and is probably close to the ancestral stock of the genus.

RESUMEN.—Un examen morfologico del "Mexican stoneroller," *Campostoma ornatum*, a lo largo de su distribución geográfica, reveló que esta especie se caracteriza en el género *Campostoma* por poseer escamas muy pequeñas, tubérculos reproductores en las hembras al igual que en los machos, y aros intestinales que raramente rodean la vejiga natatoria. *C. ornatum* es extredamente variable en ambas merística y morfometría, aunque poblaciones de la parte sur de su distribución tienden a ser mas consistentes en el sentido de que tienen menos escamas y cuerpos mas llenos. Debido a su extrema y bastante irregular variabilidad de drenaje en drenaje, taxones intraespecíficos, incluyendo a *C. ornatum pricei* no se pueden reconocer. *C. ornatum* exhibe varias caracteristicas generalizadas que probablemente lo coloquen filogenéticamente cerca del antepasado de dicho género.

The genus *Campostoma* is a closely allied group presently comprising three species, all of which are morphologically similar. The wide-ranging North American *C. anomalum* (Rafinesque) is in part sympatric with *C. oligolepis* Hubbs and Greene in the upper Mississippi valley (Burr and Smith, 1976), but also occurs as far south as northeastern México. A third species, *C. ornatum* Girard occurs chiefly in west-central México and is allopatric to *C. anomalum*.

Published information on the species is primarily limited to faunal reports and checklists. An exception is Rutter's (1896) observation that in specimens from Rucker Canyon, Arizona, and the Río Conchos, Chihuahua, the intestinal loops do not encircle the air bladder, an observation of considerable interest since the generic diagnosis has largely been based on this peculiarity. This statement and the questionable status of the nominal *C. ornatum pricei* Jordan and Thoburn prompted a review of the species.

In this paper I summarize the systematics and distribution of *C. ornatum*, compare the species with other members of the genus, and discuss its geographic variation.

METHODS

Specimens were assembled from all localities known for *Campostoma ornatum*, except for a few records for which the specimens could not be located. Counting and measuring procedures followed Hubbs and Lagler (1958: 19-26) except that number of scales above the lateral line was from lateral line to lateral line just anterior to the dorsal fin. Terminology and counting procedures for the cephalic lateral line follow Illick (1956). Measurements were made with dial calipers to the nearest 0.1 mm. All measurements were converted arithmetically. Measurements are expressed in thousandths of standard length (SL) or of head length (HL). Proportional measurements were limited to adult specimens measuring 60 mm or more in SL. Gill rakers were counted on the right side of the body and were made on the first arch.

TABLE 1. Frequency distribution of lateral line scales in selected populations of *Campostoma ornatum*.

Drainage	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	N	Mean
Río Sonora													2	2	4	3	1	2	1	3	2											20	69.8
Río Moctezuma	1		1	2	3	2	2			2	2	1	3	1	1		1										1					22	61.7
Río Yaqui									1			5	5	6	3	3	7	6	7	2	7	4	2									59	70.3
Río Papigochic									3		2	7	6	7	5	8	4	1	4	3			1	1								52	65.1
Río Casas Grandes									1	3		2	4	4	4	3	4		4	2	1											32	68.1
Río del Carmen																		1	4	4	3	1	1	2	2	2						20	74.6
Río Santa Isabel																			2		2	4	5	3	4	3	3	1		1	1	30	77.4
Río Grande												1		3	3		5	3	3	4	6	4	2	2	2							38	72.3
Río Conchos														4	3	2	5	4	6	6	4	5	2	1	1	2	2					47	72.5
Río Urique													2		2	1			4	2	3	2	2	2								20	72.5
Río Matamoros												1	1	3		3	4	6	2	2	1	1			1							25	70.5
Río Valle de Allende												2	1	2	2	3	4	2	3	1		1	1	1								23	69.2
Río Florido												1	3	1	6	4	12	2	7	4	7	4	3	2			1	1				58	71.6
Río Nazas		1	1		4	3	7	6	5	6	6	9	5	5	4	2			3													67	63.5
Río Miravalle			1		3	1	3		1	1	3		2	3	1	1																20	62.8
Río Trujillo					3	1	5	2	2	5	6	6	8	4	3	3	1	1														50	64.3

Material deposited in the following institutions was examined (abbreviations used throughout the text): Arizona State University (ASU), California Academy of Sciences (CAS), Stanford University (SU), now at CAS, Field Museum of Natural History (FMNH), Illinois Natural History Survey (INHS), University of Kansas, Museum of Natural History (KU), University of Texas, Texas Natural History Collection (TNHC), Tulane University (TU), Universidad Autónoma de Nuevo León (UANL), University of Michigan Museum of Zoology (UMMZ), and National Museum of Natural History (USNM).

MEXICAN STONEROLLER
Campostoma ornatum Girard

Campostoma ornatum Girard, 1856: 176 (original description; Chihuahua River and a tributary a few miles long, México). Girard, 1859: 41, pl. 25, figs. 1-4 (redescription; synonymy). Günther, 1868: 183 (brief description). Jordan and Copeland, 1876: 146 (listed). Jordan, 1878: 418 (listed). Jordan and Gilbert, 1883: 149 (diagnosis). Jordan, 1885: 808 (listed). Evermann and Kendall, 1894: 75, 83, 86, 89-91, 98 (listed; discussion of type). Woolman, 1894: 57, 61 (localities; tabulated measurements). Jordan and Evermann, 1896a: 205 (description; in key). Jordan and Evermann, 1896b: 243 (listed). Rutter, 1896; 259-260 (description; *C. pricei* a synonym; intestine not coiled around air bladder). Evermann and Goldsborough, 1902: 146 (Sierra Madre Mountains, Chihuahua and Colonia García, México). Meek, 1902: 41, 123 (habitat; localities in México; general range). Meek, 1903: 774, 776 (distributional pattern in México). Meek, 1904: xxxi, xxxii, xxiv, xxxviii, 41-42 (description; synonymy; in key; range; ripe female in May). Regan, 1906-1908: 149 (description; synonymy; range). Pratt, 1923: 65 (brief description; in key; Arizona). Fowler, 1924: 389 (in part). Jordan, Evermann, and Clark, 1930: 146 (in checklist). De Buen, 1940: 23 (synonymy; range). Hubbs, 1940: 10 (Terlingua Creek, Big Bend Region, Texas). De Buen, 1947: 272, 298, 319-320, 325 (synonymy; range; zoogeography). Alvarez, 1950: 46 (in key). Baughman, 1950: 130 (Texas). Jurgens and C. Hubbs, 1953: 13 (listed; range in Texas). Knapp, 1953: 51, 59 (in key; probable occurrence in Texas). C. Hubbs, 1954: 284 (Tornillo Creek, Texas). C. Hubbs, 1957a: 99 (Chihuahuan Biotic Province, Texas). C. Hubbs, 1957b: 7 (listed; range in Texas). C. Hubbs and Springer, 1957: 313 (mentioned). Eddy, 1957: 71 (key characters; figure). Moore, 1957: 138 (in key; range in United States). Miller, 1958: 214 (*C. ornatum* dispersed from Río Grande to Río Yaqui by stream capture). C. Hubbs, 1958: 7 (listed; range in Texas). Bailey et al., 1960: 13 (in checklist). Branson, McCoy, and Sisk, 1960: 220 (localities in Sonora, México). C. Hubbs, 1961: 7 (listed; range in Texas). John, 1964: 112 (Rucker Canyon, Ari-

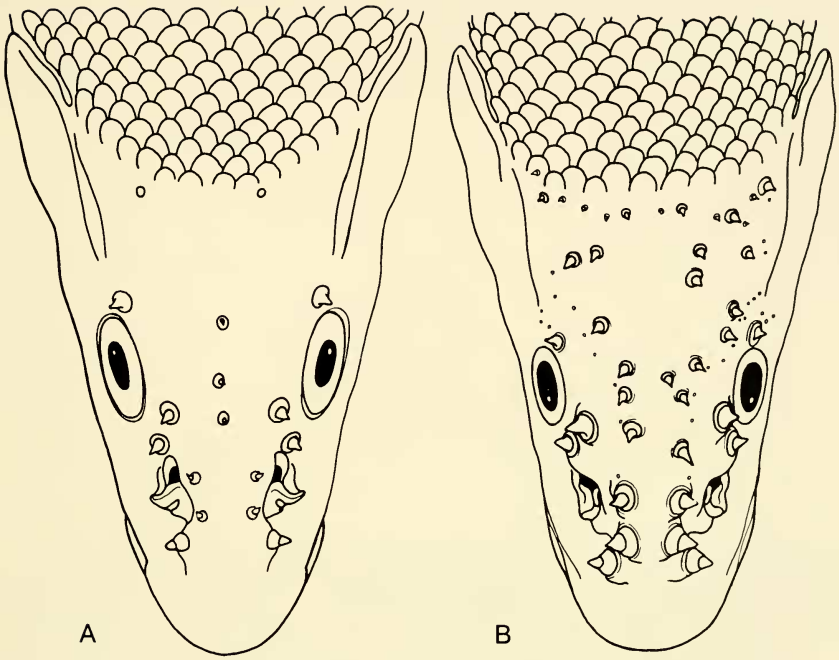

Fig. 1. Head tuberculation in breeding *Campostoma ornatum*. A) Female (UMMZ 189085) B) Male (UMMZ 161715).

zona). Miller and Lowe, 1964: 142 (range in Arizona; *C. pricei* a synonym). Anonymous, 1966: F-39 (peripherally endangered in United States). Metcalf, 1966: 139 (origins; zoogeography). Anonymous, 1968: FP-39 (peripherally endangered in United States). Minckley and Deacon, 1968: 1430 (unrealistic inclusion as an endangered species since it is only peripheral to the United States). Moore, 1968: 89 (in key; range in United States). Contreras-Balderas, 1969: 297 (Río Concepción, Sonora). Alvarez, 1970: 67 (in key; range in México). Bailey et al., 1970: 19 (in checklist). Minckley, 1971:184 (in key). Pflieger, 1971: 377 (ancestral stock). C. Hubbs, 1972: 3 (listed; range in Texas). Miller, 1972: 242 (rare in Arizona and Texas). C. Hubbs and Wauer, 1973: 376-379 (seasonal changes in Tornillo Creek, Texas). Anonymous, 1973: 69 (peripherally threatened in United States). Minckley, 1973:141 (in synonymy).

Campostoma pricei Jordan and Thoburn *in* Jordan and Evermann, 1896a: 205 (original description; Rucker Canyon, Chiricahua Mountains, southern Arizona). Jordan and Evermann, 1896b: 243 (listed). Rutter, 1896: 259-260 (synonym of *C. ornatum*). Meek, 1904: 41 (synonym of *C. ornatum*). Regan, 1906-1908: 149 (synonym of *C. ornatum*). Jordan, Evermann, and Clark, 1930: 147 (in checklist). Schrenkeisen, 1938: 156 (Arizona). De Buen, 1940: 23 (synonym of *C. ornatum*). Hubbs, 1940:10 (reference to type-locality). De Buen, 1947: 272 (synonym of *C. ornatum*). Böhlke, 1953: 30 (holotype SU 1177). Moore, 1957: 138 (Rucker Canyon, Arizona). Miller and Lowe, 1964: 142 (synonym of *C. ornatum*). Moore, 1968: 89 (Rucker Canyon, Arizona). Minckley, 1973: 141 (in synonymy).

Campostoma ornatum pricei: Minckley, 1973: 82, 141-142 (brief description; habitat; in key; male and female figured; distribution and extinction in Arizona). McNatt, 1974: 275-276 (status in Río Yaqui, Arizona).

Types.—Girard (1856) did not designate a type for *Campostoma ornatum*, but in a later publication (Girard, 1859) cited a syntypic series with data as follows: USNM 77 (4 specimens) Chihuahua River (=Río Conchos), and a tributary only a few miles long, México, collected 1855 by John Potts. One set of pharyngeal arches (USNM 2682) is part of the syntypic series (Girard, 1859). An additional label in the jar (USNM 15388) is also present but is apparently in error. Girard's

TABLE 2. Frequency distribution of body circumferential scales in selected populations of *Campostoma ornatum*.

Drainage	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	N	Mean
Río Sonora									1	1	3	6	3	2	1	1	1	1				20	55.8
Río Moctezuma					1	3	5	4	4		2											19	50.8
Río Yaqui								1	14	11	11	11	5	4		1						58	53.9
Río Papigochic					1			1	9	9	13	2	3	6	1	2	1					48	54.2
Río Casas Grandes							1		7	6	6	8	2	2								32	53.8
Río del Carmen								1	4	3	3	4	2	1	1	1						20	54.3
Río Santa Isabel													2	1	5	4	7	4	3	3	1	30	59.9
Río Grande									5	6	10	5	6	1	2		1					36	54.5
Río Conchos									5	5	11	5	10	4	5	1	1					47	55.1
Río Urique							1	1	4	3	4	5	1	1								20	53.6
Río Matamoros									1	3	4	4	3	4	5	1						25	55.7
Río Valle de Allende									7	5	5	3	1	1	1							23	53.7
Río Florido							1	1	1	3	10	9	9	10	6	4	4					58	55.9
Río Nazas	1	2	2	7	15	13	11	8	3	1	3	1										67	49.2
Río Miravalle		3	2	4	6	2	3															20	47.6
Río Trujillo			2	1	2	7	7	7	5	7	6	3	3									50	52.5

(1859) drawing of one of the syntypes is said to be "life size" and measures about 105 mm SL. While it is not specifically designated as the type, one of the USNM series measures very close to Girard's illustration (ca. 105.5 mm SL). It is also the only specimen with the pharyngeal arches removed. The other three specimens are much larger or smaller (91-114 mm SL). Based on these data, the above-mentioned specimen is herewith designated lectotype. The other three syntypes become paralectotypes (USNM 214999).

Counts for the lectotype are as follows: lateral line scales 76; body circumferential scales 52; predorsal scales 32; and caudal peduncle scales 27. The head tubercle pattern is as in Figure 1; a black band of pigment occurs in the anal, dorsal, pelvic, and pectoral fins.

The holotype of *Campostoma pricei* Jordan and Thoburn (SU 1177) is a full nuptial male 76.7 mm SL, collected by William W. Price from Rucker Canyon, Chiricahua Mountains, Cochise County, southern Arizona. Counts for the holotype are as follows: lateral line scales 72; body circumferential scales 53; predorsal scales 32; anal rays 7, not 8 (Jordan and Evermann, 1896a). The chief differences used for distinguishing *pricei* from *C. ornatum* were head length (=.278 standard length) and snout length (=.102 standard length). In the holotype the values for head length and snout length are larger than those of other breeding males measured from Rucker Canyon; however, they are not significantly different from other populations.

Diagnosis.—A species of *Campostoma* distinguished by a combination of the following characters: lateral-line scales 54-84 (usually 58-77; Table 1); body circumferential scales 44-64 (usually 47-60; Table 2); usually with 20-23 scales above the lateral line; predorsal scales 25-40 (usually 27-36; Table 3); caudal peduncle scales 23-32 (usually 24-31; Table 4); sum of lateral-line and body circumferential scales 104-145 (usually 107-135; Table 5); gill rakers on the first arch 14-20 (Table 6). Breeding males without tubercles on the nape and anterolateral portions of the body (Fig. 1). Gravid females often with tubercles (Fig. 1). Head long with somewhat acute snout (Fig. 2). Intestinal loops rarely coiling around posterior portion of air bladder.

TABLE 3. Frequency distribution of predorsal scales in selected populations of *Campostoma ornatum*.

Drainage	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	N	Mean
Río Sonora						1	4	5	2		1	1					14	32.2
Río Moctezuma				1	2	1	2	1	1								8	30.4
Río Yaqui						7	15	14	3	5	5	1					50	32.1
Río Papigochic					1	11	14	11	3	5							45	31.4
Río Casas Grandes						4	13	6	7	2							32	31.7
Río del Carmen						1	3	3	8	3				1	1		20	33.1
Río Santa Isabel							3	4	6	5	3	6	2	1			30	34.1
Río Grande						1	5	4	2	5	2	1	1				21	33.0
Río Conchos						1	6	4	9	8	5	3	1	1			38	33.4
Río Urique						1	2	5	4	1	4	3					20	33.3
Río Matamoros						4	5	6	6	2							23	31.9
Río Valle de Allende					1	4	3	3	3	2	3	2	1				22	32.7
Río Florido						2	4	6	4	8	5	1	1	1		1	33	33.5
Río Nazas	2	2	10	11	17	15	7	3									67	28.9
Río Miravalle		1	4	2	2	4	1										14	28.5
Río Trujillo			6	8	9	10	10	4	2	1							50	29.7

Description.—Scale counts, gill raker counts, and body proportion values appear in Tables 1 to 7. General physiognomy, pigmentation, and tuberculation are shown in Figure 2, details of male and female head tubercle patterns in Figure 1. An extremely variable species of moderate size (the largest specimen examined is 114 mm SL).

Dorsal and pelvic rays number 8, with no deviations observed. Caudal rays are usually 19, sometimes 18 or 20. Anal rays number 7, rarely 8. Pectoral rays number 16 to 18. Body circumferential scales number (18) 20-23 (24), modally 22,

TABLE 4. Frequency distribution of caudal peduncle scales in selected populations of *Campstoma ornatum*.

Drainage	23	24	25	26	27	28	29	30	31	32	N	Mean
Río Sonora		1	3	2		2					8	25.9
Río Yaqui		2	1	4	9	4		1			21	26.8
Río Papigochic		2	3	5	8	7	4	3	1		33	27.3
Río Casas Grandes			5	2	3	1	1				12	26.3
Río del Carmen				5	4	3					12	26.8
Río Santa Isabel							8	5	8	5	26	30.4
Río Grande				2	5	4	3	1			15	27.7
Río Conchos				3	3	5	3	2	2	1	19	28.4
Río Matamoros		1	3	7	5	2	1	1			20	26.6
Río Valle de Allende				2	4	3	2	1			12	27.7
Río Florido		1	1	5	6	7	3	6		1	30	27.9
Río Nazas	1	1	7	9	5	5	4	1			33	26.6
Río Trujillo	2	6	13	7	7						35	25.3

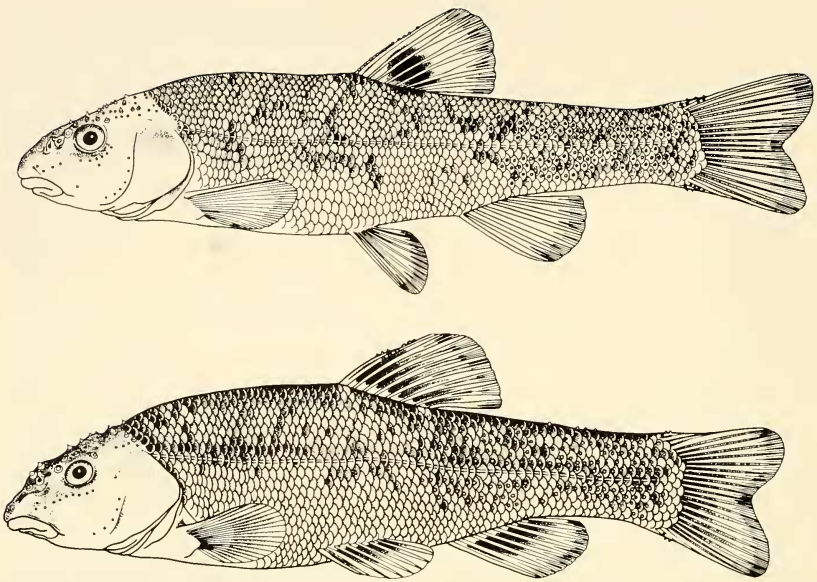

Fig. 2. Breeding adult males of *Campostoma ornatum*. Upper) UMMZ 157248, 84.0 mm SL; Río Sonora dr., 9 March 1940. Lower) UMMZ 189085, 91.5 mm SL; Río Nazas dr., 8 April 1968. Note differences in body proportions and extent of pigmentation in fins.

above the lateral line and (25) 27-34 (38) below (mode varying considerably from drainage to drainage). Caudal peduncle scales are 10 to 15 above the lateral line and 11 to 15 below. The pharyngeal tooth count from throughout the range is 0,4—4,0 in 30 specimens. Gill rakers are moderately long, well separated, and number 14 to 20.

The snout is usually acute and rounded, and projects slightly beyond the mouth. The mouth is ventral and rounded, with the lower lip having a distinct cartilaginous ridge not covered by skin. The premaxilla is protractile. The eye is small and located rather high on the head. The body is rather stout. Fins are of moderate size and angulation. The anterior rays do not exceed the length of the posterior rays in the depressed dorsal fin. The pelvic fins in breeding males usually reach the insertion of the anal fin. The posterior border of the dorsal fin is usually straight, that of the anal fin is rounded. The dorsal fin is inserted directly above or slightly behind the pelvic fin insertion.

The lateral line is straight and is usually complete, but occasionally pores are lacking on posterior scales. The cephalic lateral line is usually complete, although the supratemporal canal may be slightly interrupted at the midline or to one side. Supratemporal pore counts range from 5 to 8; the supraorbital canal pores, from 8 to 11; infraorbital canal pores, from 13 to 17; preoperculomandibular canal pores, from 9 to 11.

The intestine is variable in length (usually 150-200 mm in specimens measuring 65-70 mm SL), but in this species, contrasting with the other two, loops were found to encircle the posterior portion of the air bladder in only 12 of 60 (20%) specimens checked. Two patterns are evident: the intestine coiling around the air bladder similar to that of *C. anomalum* (Kraatz, 1924) only with the coiling less extensive; an antero-posterior folding below or to the side of the air bladder

TABLE 5. Frequency distribution of the sum of lateral line and circumferential scales in selected populations of *Campostoma ornatum*.

Drainage	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123
Rio Sonora																1	1	1	3	4
Rio Moctezuma			2	3	3	1				2	1	2		1		1	1	1	1	
Rio Yaqui														1	3	3	4	5	5	3
Rio Papigochic										1			1		4	7	6	6	2	5
Rio Casas Grandes										1	1		1		2	1	5	3	4	2
Rio del Carmen																				
Rio Santa Isabel																				
Rio Grande																1		2	2	3
Rio Conchos																		1	2	4
Rio Urique																1	2	1	1	1
Rio Matamoros																1	2	2		
Rio Valle de Allende													1			4	2	3	1	3
Rio Florida													1				1		4	3
Rio Nazas	2	1	2	3	5	3	5	4	2	8	8	7	4	5	3	1	1	1	1	1
Rio Miravalle	4	1	1	2	1		2			1	2	2	3	1						
Rio Trujillo				1	1	3	2	1	2	3	2	2	2	9	3	3	4	4	2	2

124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	N	Mean
1	1		2		2	1	1			2												20	125.4
																						19	112.4
7	3	6	3	6	4	2	2			1												58	124.3
4	4	3			2	1		1	1													48	122.2
3	4	2	2		1																	32	121.9
2		3	3	3	2	2		2			.3											20	128.9
						1	3	1		3	4			5	4	3	1	3			2	30	137.3
1	1	5	5	3	3	3	4	2			1											36	127.0
6	4	3	4	4	4	4	6	1	1				1	1	1							47	127.7
1		3	2	2		2	3	1														20	126.1
3	1	4	2	5	2			1	1		1											25	126.2
3	1	2			1	1			1													23	122.9
7	4	4	4	8	5	5	2	2	4	1	1					1	1					58	127.6
																						67	112.9
																						20	110.3
1	1		1																			50	114.5

with one or at most two loop folds around the air bladder but not entirely encircling it. These conditions are evidently the result of the intestine being shorter in this species than in the other two. Both intestinal conditions may occur in one sample but do not vary geographically. Rutter (1896), upon examining specimens from Rucker Canyon, Arizona, and the Río Conchos, Chihuahua, reported that in none did intestinal loops entirely encircle the air bladder. The peritoneal color ranges from dark brown to black.

Coloration is extremely variable both ontogenetically and among adults. Most adults have the characteristic mottled coloration of the genus as described by Cross (1967) for *C. anomalum*. Juveniles tend to lack heavy mottling but often have a dark lateral stripe extending from the snout to the caudal peduncle, termi-

TABLE 6. Frequency distribution of number of gill rakers on the first arch in selected populations of *Campostoma ornatum*.

Drainage	14	15	16	17	18	19	20	N	Mean
Río Sonora				4	3	4	3	14	18.4
Río Yaqui		3	3	8	4	2		20	17.0
Río Papigochic	3	5	7	4	1			20	15.8
Río Santa Isabel	2	2	7	7	2			20	16.3
Río Florido	2	2	8	5	2	1		20	16.3
Río Nazas		4	7	5	2	1	1	20	16.6
Río Trujillo	1	8	8	3				20	15.7

nating in a slight basicaudal spot. Mottling when developed in juveniles is usually dorsal (within and above the lateral stripe). Fins are usually transparent in both sexes during non-breeding seasons but a black band of pigment may appear in the dorsal fin several months prior to, and continuing through, the spawning season.

Nuptial tuberculations.—Campostoma ornatum contrasts with the two other species of *Campostoma* in having no tubercles on the nape or on the anterolateral sides of the body, in having small granular tubercles on the posterolateral sides of the body, and in having head tubercles on females.

Tubercle patterns on the head are very similar to those in *C. anomalum* (Burr and Smith, 1976: Fig. 3) and are large and erect (Fig. 1). The sides of the head (cheek and opercle) usually lack tubercles. The lower edge of the operculum, gill membranes, and the area dorsal to the upper lip are covered with minute whitish tubercles. Body tuberculation begins around the posterior edge of the dorsal fin (sometimes slightly before) and extends posterolaterally on to the caudal peduncle, often outlining the upper and lower rudimentary caudal rays. Most scales above the lateral line bear one tubercle per scale although some individuals have two per scale. The scales on the caudal peduncle below the lateral line have one tubercle per scale. The dorsal fin is tuberculate along the anterolateral edges of the rudimentary ray, and the branches of rays 2 through 4 are tuberculate. Pectoral rays 2 through 4 have a single file of tubercles basally, and the 2nd and 3rd rays have a double file distally; the 5th pectoral ray sometimes is sparsely tuberculate. The pelvic and anal fins lack tubercles.

On large breeding males (about 70 mm SL) a crescent-shaped row of 3 retrorse tubercles lies between the nostrils on a swollen portion of the snout. Another line of 2 to 4 tubercles arises anterodorsally to the eye and extends posteriad, with many small tubercles between the eyes and on the head, sometimes bordering the edge of the nape. In small specimens (40-50 mm SL) the tubercles between the nostrils and above the eye are usually the only ones present, although the pectoral fins may be almost fully tuberculate.

This is the only species of *Campostoma* in which tubercles have been reported on females. Characteristically, females of *C. ornatum* have 1 to 3 small white tubercles in a crescent-shaped row above the nostril (the snout does not become

swollen) and from 1 to 4 tubercles in a line around the orbit. A few tubercles are scattered on the head and between the eyes (not as extensively as in males). No tubercles have been observed elsewhere on the fins or bodies of females. Tubercles have been recorded only on females longer than 50 mm SL and usually gravid.

Breeding coloration.—In preserved breeding males, the dorsal and anal fins often have a velvet-black medial band (Fig. 2). On the pectoral and pelvic fins black pigment is heavily concentrated on the distal edges and becomes less intense proximally. The black caudal spot lengthens transversely and often appears as a dark vertical band of pigment.

On a color slide of a breeding male (courtesy of R. R. Miller, pers. comm.), the distal half of the dorsal fin is milky white, basally the fin is orange, and medially it is velvet-black. The anal fin is similar to the dorsal fin but has less black. The caudal fin is mostly milky white, with black and orange confined to the basal one fourth. The edge of the shoulder girdle is blackened. Jordan and Thoburn, in their original description of the nominal *C. pricei* (Jordan and Evermann, 1896a), described breeding coloration as "fins all flushed with red (in spring males)." Girard (1859) stated that the fins in *C. ornatum* have black patches at their bases and are otherwise orange or yellowish brown. Apparently, breeding coloration is similar to that described for *C. anomalum* (Cross, 1967).

In breeding females only the dorsal fin develops a black band. No information is available on orange-red coloration in females.

Sexual dimorphism.—No sexual dimorphism among meristic characters was found. Males attain a greater length than females; the largest male examined measures 114 mm SL; the largest female, 80 mm SL. The dorsal, pectoral, pelvic, and anal fins are noticeably more expanded and longer in breeding males than in gravid females. In addition, the lips and the snout region of the breeding males become swollen during the breeding season. These characteristics are not expressed among females. In fully gravid females (as in ASU 6276 and UMMZ 157248) the body becomes greatly distended in depth and width.

Geographic variation.—*Campostoma ornatum* is noteworthy for being one of the most variable cyprinids thus far investigated in México, and yet is remarkably conservative throughout its range in such features as pharyngeal tooth number, fin ray counts, and several body proportions. Frequency distributions for meristic characters examined by drainage systems are given in Tables 1 to 6. Meristic characters were analyzed initially by river system, but have been combined into major drainages when no significant intradrainage variation was noted. Interdrainage variation in body proportions of breeding males is summarized in Table 7.

In general, mean values of meristic and morphological characters increase from south to north. The overall pattern is obscured by populations in the Río Santa Isabel (at General Trías) which have high scale numbers, and populations in the Río Moctezuma which have low scale numbers.

Gill-raker number and mottled body coloration tend to increase from east to west, whereas, body depth tends to decrease from east to west. Populations in the Ríos Nazas and Trujillo have the deepest bodies and have fewer mean numbers of gill rakers, whereas, the populations in extreme western México (Río Sonora) have the slenderest bodies and the highest mean number of gill rakers. Populations farther east than the Río Sonora, such as those in the ríos Yaqui, Casas Grandes, and Papigochic, are also heavily mottled and show a mean average increase westward in the number of gill rakers.

Scale counts are extremely variable within a stream system as well as between drainages but show some patterns, as described above. The two characters found to be the most variable were the numbers of lateral-line scales and of circumfer-

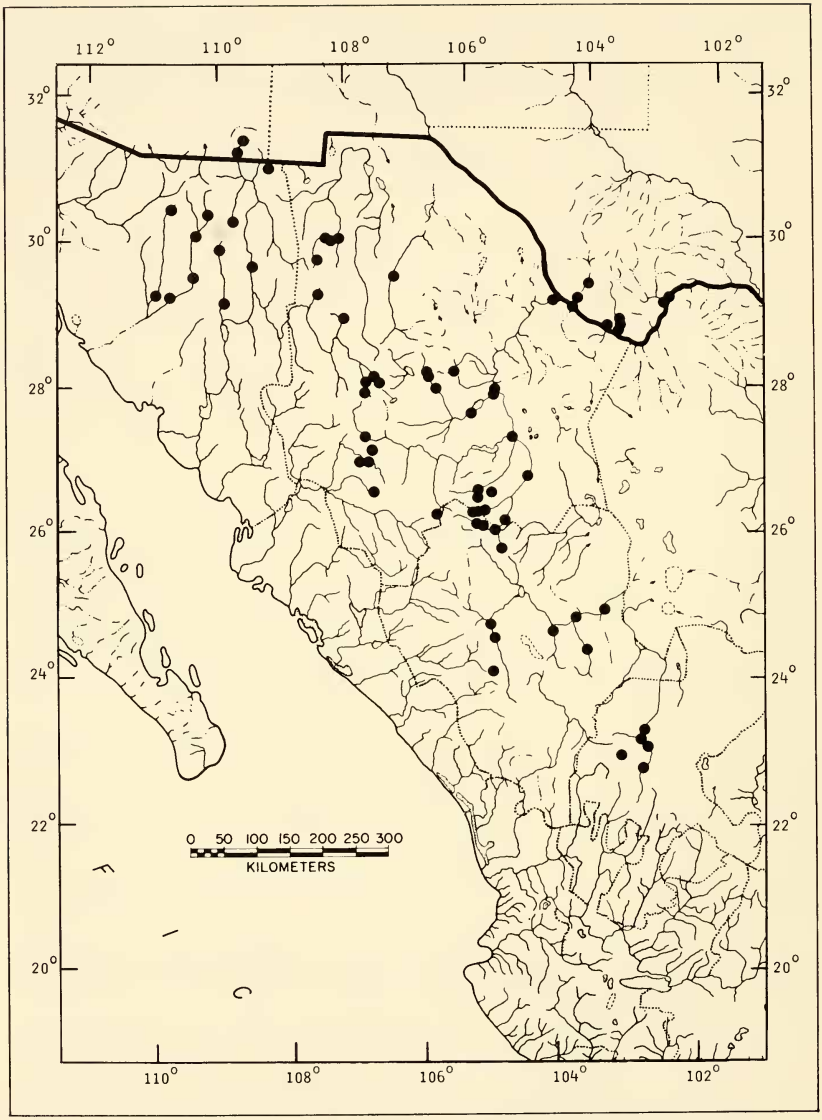

Fig. 3. The distribution of *Campostoma ornatum*. Broadly overlapping symbols are not plotted.

ential scales. The rather marked tendency for only southern populations (ríos Nazas, Trujillo, Miravalle) to have low scale numbers is obscured by the peculiar situation in the Río Moctezuma in which similar, low scale counts were found. The similarity between these geographically widely separated populations breaks down somewhat in number of body circumferential scales, number of predorsal

TABLE 7. Proportional measurements (expressed in thousandths of SL and HL) that show interdrainage variation in full nuptial males of *Campostoma ornatum*. Range is given above, mean below.

Character	Río Nazas	Río Conchos	Río Papigochic	Río Casas Grandes	Río Sonora	Río Yaqui
N	11	12	14	11	5	7
SL (mm)	60.0-91.5 75.8	60.3-92.0 76.2	65.4-90.1 75.3	66.0-104.4 82.1	73.4-88.9 80.4	76.6-94.2 87.1
Body Depth/SL	231-263 248	209-254 231	203-263 239	216-263 236	215-246 227	209-254 230
HL/SL	253-311 283	234-298 267	261-289 281	264-296 273	265-283 271	256-284 273
Snout Length/SL	82-118 97	75-100 84	82-104 93	72-105 87	88-102 92	84-102 94
HL (mm)	16.8-26.8 21.5	15.7-24.5 20.3	18.6-24.9 21.1	17.4-28.7 22.5	19.7-23.6 21.8	20.2-26.2 23.8
Snout Length/HL	279-389 341	261-358 313	314-371 332	278-383 322	309-379 339	321-366 344
Head Width/HL	448-514 480	412-527 477	435-540 485	333-535 472	466-517 492	478-550 508
Interorbital Width/HL	170-231 199	155-218 181	175-226 195	155-256 201	174-204 191	200-218 207

scales, and number of caudal peduncle scales. The Río Moctezuma is a tributary of the Río Yaqui in which populations otherwise show typically northern scale counts. Although the more northern population in the Río Moctezuma has apparently been isolated from the Río Yaqui by an ancient lava field (of unknown geological age), the more southern population of this river transgresses this geological feature and thus its low scale numbers cannot be explained by geographic isolation.

The Río Santa Isabel population is unusual in having consistently high scale numbers; all individuals are heavily mottled, but they are intermediate in gill raker number. Again, there is no evident explanation for this combination of characters.

Southern populations of *C. ornatum* are deeper bodied and longer snouted, but this trend is disrupted by deeper bodied, long-snouted populations in the Río Papigochic. The most slender-bodied populations are those from the Río Sonora, which also have long heads and snouts. Rucker Canyon populations have rather large heads, expressed in characters measured such as bony interorbital width, head width, and head length, which in part were the primary differences used by Jordan and Thoburn to distinguish the nominal *C. pricei* from *C. ornatum* (Jordan and Evermann, 1896a). Body size was individually variable and specimens from all major drainages had similar SL measurements. The largest specimen examined (114 mm SL) was from the Río Conchos. The populations examined from the Río Grande, Río del Carmen and Río Moctezuma were all less than 66 mm SL, the majority less than 45 mm SL. Since there is some seasonal variation in population density in the Río Grande tributaries (C. Hubbs and Wauer, 1973; Gehlbach, pers. comm.) and the Río del Carmen often dries up (Meek, 1904), it may be that large adults do not ascend into these streams or perhaps the fluctuation in stream size does not produce enough resources for a substantial buildup of population size.

Coloration among adult populations from the ríos Nazas and Trujillo varies from almost no mottling to scattered dark patches of pigment both dorsally and ventrally. Populations from the ríos Yaqui, Sonora, and Casas Grandes have dark base colors and are heavily mottled. One population, from Río Sonora (UMMZ 157248), deviates considerably from the typical fin pigmentation pattern already

described in that pigmentation is conspicuously lacking in all fins except the dorsal (Fig. 2). The males in this collection are highly tuberculate and the females are very ripe. The differences in coloration in *C. ornatum* are probably a response to contrasting environments as has recently been shown to be characteristic of other Mexican cyprinids (Hubbs and Miller, 1975).

Although some populations of *C. ornatum* maintain several features that initially appear to warrant taxonomic recognition, the species is subject to considerable local variation in an overall discordant pattern. Additional collections of breeding material and comparative life history studies may eventually justify a reappraisal of the status of the populations in the Río Nazas, Río Trujillo, Río Moctezuma and the Río Santa Isabel, but at present the variation defies any objective breakdown into species or even subspecies. Until more conclusive evidence is available, it is proposed that the species be treated as one highly variable entity and that use of the subspecific name *pricei* be discontinued.

Comparisons.—Campostoma ornatum differs trenchantly from *C. anomalum* and *C. oligolepis* (Table 8). The overlap in certain scale counts between *C. ornatum* and *C. anomalum* does not complicate the specific separation, since *C. anomalum* populations with the highest scale counts are generally those that approach the geographic range of *C. ornatum* where scale counts are high. *Campostoma anomalum* populations with low scale counts (the nominate *C. anomalum*) are geographically widely separated from those populations of *C. ornatum* having the lowest scale counts.

In addition to the differentiae treated in Table 8, *C. ornatum* and *C. anomalum* show subtle and average differences, best perceived after handling many specimens. *Campostoma ornatum* usually has a stouter, deeper body, a narrower head, narrower interorbital, and smaller mouth. It is also smaller.

Besides having more gill rakers, *C. anomalum* exhibits a rather high incidence of a peculiar structure of the rakers: they are Y-shaped, due to bifurcation at or near their tips. Each arch may bear from one to several anomalous rakers.

Campostoma oligolepis is readily distinghished from *C. ornatum* by its low scale numbers, its higher gill raker numbers and its unique tubercle pattern (Burr and Smith, 1976).

Distribution.—Campostoma ornatum is widepread in México, occurring on both slopes of the Sierra Madre Occidental, with its center of distribution in the states of Chihuahua, Sonora, and Durango. It is abundant in the Río Grande-Río Conchos drainages in Chihuahua and Durango (Río Florido) and the Río del Fuerte drainage in southwestern Chihuahua, as well as the streams that drain Lago de Guzman and Lago de Palos (Río Casas Grandes and Río del Carmen, respectively). In Sonora, it occupies tributaries of the Río Yaqui, Río Papigochic and the Río Sonora. Rather isolated populations occur in Durango in tributaries of the Río Nazas and Río Piaxtla, and in the state of Zacatecas in the Río Trujillo. Woolman's (1894) record for Río Lerma, Salamanca, Guanajuato is apparently in error (Meek, 1904). The species still occurs in the Big Bend Region of Texas, although it is absent during some months of the year in Tornillo Creek (C. Hubbs and Wauer, 1973) and Terlingua Creek (Frederich R. Gehlbach, pers. comm.). It is still common in Rucker Canyon and Leslie Creek, Arizona (McNatt, 1974), even though Minckley (1973) considered it extinct (specimens collected as late as 1974 have been examined from Rucker Canyon and Leslie Creek). The apparent preference of *C. ornatum* for headwater situations may account for its absence in collections from mainstream habitats.

Meek (1904) and Miller (1958) indicated that stream capture may perhaps explain the presence of Río Grande fishes in the Río Yaqui. According to Miller (1958), the Río Conchos may have been captured by the Río Papigochic (of the Yaqui system) 44.8 km (28 airline miles) south of Miñaca, Chihuahua. Also, the

TABLE 8. Summary of Primary Differences Distinguishing *Campostoma ornatum*, *C. anomalum*, and *C. oligolepis*.

Character	*C. ornatum*	*C. anomalum*	*C. oligolepis*
Circumferential scales	Usually 47-60	Usually 36-48	Usually 31-36
Scales above the lateral line	Usually 20-23	Usually 17-20	Usually 13-16
Predorsal scales	Usually 27-37	Usually 18-25	Usually 16-20
Lateral line scales	Usually 58-77	Usually 46-56	Usually 43-47
Sum of lateral line and circumferential scales	Usually 107-135	Usually 83-104	Usually 74-82
Tubercles on nape and antero-lateral sides of breeding males	Absent	Present	Present
Small tubercles on snout and above eye of breeding females	Present	Absent	Absent
Snout shape	Somewhat acute	More blunt and rounded	Longer and more globose
Intestinal loops coiling around air bladder	Very rarely	In majority of specimens (Kraatz, 1924)	In majority of specimens (Hubbs and Greene, 1935)
Gill rakers on first arch	14-20	21-35	19-26

Río Papigochic may have formerly formed the headwaters of the Río Casas Grandes. The circumstance that the *C. ornatum* morphotypes occurring in the Río Papigochic, Río Yaqui, and the Río Casas Grandes are very similar seems to substantiate this route of dispersal as highly probable.

Presumably, additional headwater crossovers, transfers, or migrations via periodically formed floodplains or overflow have also taken place, since *C. ornatum* (and other Río Grande types) are present in coastal drainages such as the Río Sonora, Río del Fuerte, and Río Piaxtla. It is noteworthy that portions of the headwaters of the Río del Fuerte (where *Campostoma* occurs) are presently in very close proximity to those of the Río Conchos, as are the headwaters of the Río Piaxtla and the Río Nazas. Meek (1904) stated that Lago de Mayran and Lago de Viesca (lakes drained by the Río Nazas and Río Trujillo, respectively) were probably connected at some former time and may have flowed northward toward the Río Conchos-Río Grande Basin, henceforth affording a dispersal route for *C. ornatum* into these drainages. Conant (1963) suggested that a succession of pluvial lakes during glacial stages may have permitted free water flow over a route similar to that suggested by Meek, thus allowing connections between the Río Grande fauna and that of ríos Nazas and Trujillo. Whatever the case, the lack of strong differentiation between ríos Nazas and Trujillo and the Río Conchos populations suggests that such dispersal has been relatively recent.

Although *C. anomalum* is known from tributaries of the Río Grande in Nuevo León, México (ríos Salado and San Juan; Alvarez, 1970), *C. ornatum* and *C. anomalum* have not been collected together and apparently maintain allopatric ranges.

Miller (1972) regarded *ornatum* as a threatened species in Texas and Arizona, presumably because of the restricted habitat (by reason of streams drying up) in

these regions. Its depletion in numbers in recent years in Texas may also have been due to competition with *Fundulus kansae* Garman (C. Hubbs and Wauer, 1973). McNatt (1974) has summarized the information on its present status in Arizona, where he reported it to be abundant in Rucker Canyon. *C. ornatum* is recognized nationally in the United States as a peripherally threatened species (Anonymous, 1973).

In México, the species distribution has evidently undergone little change since Meek's (1904) report on the freshwater fishes of that region. *Campostoma ornatum* is presently abundant at many localities in north-central México (more than 300 specimens have been collected at several sites: KU 8411, UMMZ 182375, UANL 477, 544, 565); and all of the localities listed by Meek have been revisited by recent workers, and the species has been found to be still common. Collections with the fewest specimens were taken in the western coastal drainages such as those of rios Sonora, Urique, and Piaxtla. Perhaps this rarity in numbers of specimens is a reflection of rather recent arrival to these drainages and the low reservoir of *Campostoma* populations that have not had time to build to suitable sizes.

Ecology.—Most Mexican stonerollers have been collected in riffles, chutes, and pools in creeks and rivers from warm, clear (sometimes slightly turbid) water and with bottom materials consisting largely of sand, pebbles, gravel, rock, and bedrock (rarely, mud). They have been taken more commonly in shallow water 10 cm to 1 m deep and apparently favor headwaters (Fig. 3). The largest collections come from gravel runs or gravel-bottom pools. Vegetation may be abundant to absent.

Nuptial males and gravid females were included in collections made from March to June in Chihuahua and Sonora and in February in Durango (Río Nazas). Males nearing full tuberculation were present in October collections made in Texas. Nuptial males ranged in size from 55-105 mm SL.

C. Hubbs and Wauer (1973) reported young individuals and breeding adults of *C. ornatum* present in January and half-grown young from May to June, in Tornillo Creek, Texas. They also remarked that the breeding season is probably in winter and spring. McNatt (1974) stated that in smaller pools in Rucker Canyon, Arizona, at least three age classes of *C. ornatum* were present. Cleared gravel areas, suggesting spawning activities, were observed in late May. The presence of tuberculate males and gravid females at different times of the year may indicate some temporal variation in spawning activities, although partially nuptial males in October and full nuptial males in February are probably only in preparation for an early spring spawning season. However, many Mexican cyprinids spawn in January and February (R. R. Miller, pers. comm.).

Cursory examination of intestinal contents suggests that the diet of *C. ornatum* is very similar to that of *C. anomalum* (Kraatz, 1923), consisting mainly of diatoms, bacteria, and algae. In the only report of predation on this species, McNatt (1974) found some in the stomachs of *Salmo gairdneri* Richardson.

Campostoma ornatum was found to be relatively free of external parasites except in one collection from the Río Trujillo (UANL 1130-51 individuals) which was heavily diseased with a monogenetic fluke. Large nemotode worms were entwined throughout the intestines of adults from Río Trujillo (UANL 1061).

Relationships.—Campostoma ornatum is most closely related to *C. anomalum.* The major features in which *C. ornatum* is divergent from *C. anomalum* are 1) development of smaller scales; 2) loss of tubercles on the nape; 3) development of head tubercles on females; 4) poorly developed intestinal coiling around the air bladder; and 5) more reduced body size. Of these features, 1 and 4 are clearly the primitive or generalized condition, and 2, 3, and 5 are probably primitive. *Campostoma oligolepis* displays several derived features (Burr and Smith, 1976) and is probably the most advanced member of the genus.

Specimens examined.—A list of specimens examined in this study may be obtained, for the cost of photocopies, from the author, the San Diego Natural History Museum Library, or the Carl L. Hubbs Library at Scripps Institution of Oceanography.

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